

Sexual Dimorphism and Interspecific Cranial Form in Two Capuchin Species: *Cebus albifrons* and *C. apella*

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ABSTRACT Ontogenetic patterns of sexual dimorphism and cranial form in two capuchin monkeys, *Cebus albifrons* and *C. apella*, are investigated by means of univariate, bivariate, and multivariate statistics. The analyses are based on 23 linear variables. Univariate analyses indicate that similar ontogenetic patterns of cranial sexual dimorphism are present; however, interspecific differences exist in timing. Ontogenetic scaling is present in both species' crania; however, it is more prevalent in *C. albifrons*. Several departures are present in cranial regions associated with orbital shape, the dental arcade, and the muscles of mastication. The latter two indicate that sexual differences in diet and/or foraging strategies may exist. Sexual selection is suggested as being the primary selective regime underlying the observed patterns of cranial sexual dimorphism in each species. Interspecific comparisons confirm that *C. apella* possesses a more dimorphic cranium than *C. albifrons* and that sexual dimorphism in *C. apella* begins earlier in development. Although interspecific ontogenetic scaling is present in some cranial variables, *C. apella* is not just a scaled-up version of *C. albifrons*. These sympatric congeners seem to be differentiated by variables related to the orbital region and the masticatory apparatus, as indicated by both departures from ontogenetic scaling and results of the discriminant function analysis. Ecological selection, rather than varying degrees of sexual selection, is likely to be responsible for this finding given that *C. apella* is known to consume hard-object foods. This is consistent with the predicted outcome of the competitive exclusion principle. Am J Phys Anthropol 104:487–511, 1997.

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The importance of studying sexual dimorphism and cranial form using samples comprised of individuals representing all postnatal stages has been extensively discussed in the literature (e.g., Shea, 1986; Leutenegger and Masterson, 1989a, b; Ravosa and Gomez, 1992). The primary advantage of using an ontogenetic sample is that adult end points are the result of selection acting upon the different developmental stages that an organism passes through as it matures from infancy through adulthood. Selection will not always be the same for each consecutive

stage; therefore, adults can be the result of different developmental processes. The idea that different morphological patterns may depend upon different developmental processes, with distinctly different evolutionary pathways, is the focal point in the study of heterochrony (Gould, 1977).

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The genus *Cebus* is comprised of four widely known species, *C. albifrons*, *C. apella*, *C. capucinus*, and *C. olivaceus*. Recently, a new untufted species was described, *C. kaapori* (Queiroz, 1992); however, after further study it has been reclassified as a new subspecies of *C. olivaceus* (Harada and Ferrari, 1996). It is possible that other valid species may exist but are currently designated at the subspecific level (Mittermeier et al., 1988; Torres, 1988; Mudry, 1990; Rylands et al., 1993; Kinzey, 1997). Although these monkeys are among the most widespread of all New World primates (Freese and Oppenheimer, 1981; Emmons, 1990; Rowe, 1996), a paucity of information exists about much of their development and morphology. Most comparative studies on *Cebus* morphology focus on dental (e.g., Teaford, 1985), mandibular (e.g., Cole, 1992), or postcranial analyses (e.g., Jungers and Fleagle, 1980; Ford and Hobbs, 1994), whereas comparatively little work has been done on *Cebus* cranial morphology (e.g., Kinzey, 1974). Hill (1960) describes many gross anatomical aspects of the capuchins but does not provide details of age-related cranial changes. At present, cranial morphology and age changes have been studied only in the white-capped capuchin, *C. capucinus* (Schultz, 1960, 1962) and more recently in the tufted capuchin, *C. apella* (Corner and Richtsmeier, 1991). Both studies provide pertinent information on sexual dimorphism and age-related changes; however, direct comparisons to the present study are not possible because of different methodologies.

Within the last decade, there has been an exciting new interest in examining the underlying causes of sexual dimorphism (e.g., Kay et al., 1988; Plavcan and van Schaik, 1992, 1997; Ford, 1994; Plavcan et al., 1995; and references within). This study will focus on two general, although not necessarily mutually exclusive, hypotheses proposed to explain sexual dimorphism: sexual selection and ecological selection (Rodman and Mitani, 1987). Sexual selection operates either by intra- or intersexual competition for mates and is based upon sexual differences in reproductive strategies (Trivers, 1972). Ecological selection produces sex differences in morphology and/or behavior by niche diver-

gence to reduce feeding competition (Selander, 1972). Sexual selection theory is cited as underlying most cases of sexual dimorphism in primates because it is more parsimonious and easier to make predictions from than the hypothesis of ecological causation. If dietary divergence between the sexes is the goal of selection, then, in addition to intersexual differences in body sizes, there may be differences in relative size or shape in the trophic structures (Shine, 1989; Leutenegger, 1992). Selander (1972) suggests that dimorphism in size or shape greater than that expected due to body-size differences alone and in a direction inconsistent with sexual selection is the only reliable evidence to support the ecological causation hypothesis. There are, however, several problems associated with determining if ecological selection underlies observed morphological differences between the sexes. Janson and Boinski (1992) point out that 1) correlational studies between morphology and diet leave significant dietary variation unexplained (Kay, 1984), 2) morphology can at best reveal only the broad limits of what a diet can be (Scheine and Kay, 1982; Milton, 1984), 3) foods with distinct processing needs are not equally abundant in a species' habitat (Sussman, 1987), and 4) food processing requires both morphology and behavior. Rose (1994) points out another potential problem in that dietary differences may be a secondary outcome of size differences caused by sexual selection. Thus, differentiating ecological from sexual selection as an underlying causal force appears to be a difficult task (Shine, 1989).

Given the available behavioral data of these two species (Defler, 1979a, b; Janson, 1984, 1986a, b), it can be said that sexual selection clearly plays a significant role in the production of both cranial and body weight dimorphism (Ford, 1994). However, the significance of ecological selection is expected to increase when examining the morphological relationships between these sympatric capuchins due to the competitive exclusion principle (Futuyma, 1986). Known differences in foraging behavior exist among the capuchins, with *C. apella* possessing a more vigorous foraging strategy (Thorington, 1967; Struhsaker and Leland, 1977;

Jungers and Fleagle, 1980; Terborgh, 1983). Likewise, dietary differences exist between the capuchin species and relate to *C. apella* eating more hard fruits, seeds, and palm nuts (Kinzey, 1974; Moynihan, 1976; Terborgh, 1983; Janson and Boinski, 1992). Comparative mandibular analyses indicate that *C. apella* possesses a more robust mandible than either *C. albifrons* or *C. capucinus* due to trophic specialization (Bouvier, 1986; Cole, 1992; Daegling, 1992). Molar microwear analyses provide further evidence of dietary differences among the various capuchin species (Teaford, 1985).

This study investigates and compares ontogenetic patterns of cranial sexual dimorphism in two capuchin species, the white-fronted capuchin (*C. albifrons*) and the tufted capuchin (*C. apella*). Univariate, bivariate, and multivariate analyses will be used to test five hypotheses: hypotheses 1 and 2 pertain to intersexual aspects of capuchin biology, whereas hypotheses 3, 4, and 5 pertain to aspects of the capuchins' evolutionary biology. Hypothesis 1 states that size dimorphism within a species will affect all regions of morphology, including the cranium. This predicts that males will possess larger means for each variable and that the male cranium will be an ontogenetically scaled-up version of the female cranium due to sexual selection. Hypothesis 2 states that ecological selection for dietary differences will affect size dimorphism in variables associated with mastication. It predicts that males of each species will possess significant variation in their masticatory apparatuses if ecological divergence has occurred. Hypothesis 3 states that, given the behavioral data of these species, *C. apella* will possess a larger degree of cranial dimorphism than *C. albifrons*. It appears that *C. apella* is subjected to a stronger degree of sexual selection than *C. albifrons*; therefore, hypothesis 3 predicts that the cranium of *C. apella* is more sexually dimorphic than that of *C. albifrons*. Hypothesis 4 states that interspecific size differences between the capuchins' crania will be the result of ontogenetic scaling. This predicts that *C. apella*'s cranium will be a larger, scaled-up version of *C. albifrons*' cranium. Hypothesis 5 states that *C. apella* will possess different cranial form

than *C. albifrons* because it lives in a slightly different ecological niche. Due to the competitive exclusion principle, hypothesis 5 predicts that *C. apella*'s cranium will possess a different pattern of cranial variation in variables associated with mastication. This pattern may include differences in variable means and/or scaling. These morphological features will help the congeners to live sympatrically in slightly different ecological niches.

MATERIALS AND METHODS

The samples

The morphometric analyses in this study are based on samples of 173 white-fronted capuchin (*C. albifrons*) and 345 tufted capuchin (*C. apella*) crania from collections housed at the American, Field, and National Museums of Natural History. The samples are geographically heterogeneous, as expected given these species' wide distributions and adaptability (Fragaszy et al., 1990). Subspecific designation was noted when available, but no analyses were performed, given that the focus of this study is on the taxonomic level of the species. Each specimen's sex was obtained from the museums' field notes. Several misclassified adult specimens were present and reclassified according to cranial and canine morphology.

Aging criteria

Reliable age estimates for individual crania are necessary for the type of ontogenetic analyses in this study. Exact chronological ages of the sample are unknown; therefore, each specimen's developmental stage was estimated on the basis of dental eruption patterns. This allows for the determination of cross-sectional growth patterns on the basis of age grouping (Cock, 1966; Shea, 1983a, b). The six developmental stages, D1–D6, are defined in Table 1 as well as the specific sample sizes of each developmental stage per species. The dental criteria used were modified from Corner and Richtsmeier's (1991) analysis of cranial form in *C. apella*. The samples are large, and in both species the number of nonadult specimens equals or outnumbered the adult specimens.

When chronological age is unknown, tooth development can provide a measure of rela-

TABLE 1. Developmental stages and sample sizes for male and female *Cebus albifrons* and *Cebus apella*

Age	Description	<i>C. albifrons</i>		<i>C. apella</i>	
		Male	Female	Male	Female
D1	Any stage of eruption up to and including the full deciduous dentition	11	6	28	11
D2	From D1 up to and including M1 reaching occlusal plane	1	0	7	8
D3	From D2 up to and including I1 reaching occlusal plane	8	3	19	12
D4	From D3 up to and including M2 reaching occlusal plane	10	13	36	27
D5	From D4 up to and including P2 reaching occlusal plane; specimens missing canines, M3, or both are included	16	19	51	29
D6	Full permanent dentition in place	43	43	67	50
	Total sample size	89	84	208	137

tive developmental age. However, relative aging techniques may introduce some aging biases into the study (Corner and Richtsmeier, 1991; Klingenberg and Spence, 1993; Smith et al., 1994). Several biases noted by Corner and Richtsmeier (1991) include 1) developmental age intervals may not be of equal length, 2) dentally precocial or altricial individuals may be misclassified, and 3) the same dental pattern may not be present for both sexes of the same developmental age group. Several points need to be addressed in the discussion of these biases. First, no assumption of equal length in the developmental age intervals both within and between species is made in the present study. Second, the misclassification of dentally precocial or altricial individuals is not a major concern because these conditions are presumably represented by a very small number of specimens (Masterson, personal observation). Finally, some data are available pertaining to times of dental eruption in both *C. albifrons* and *C. apella*.

Fleagle and Schaffler (1982) examined mandibular tooth development and eruption times in a captive colony of *C. albifrons*. Male white-fronted capuchins are precocious in both development and eruption relative to females, but the differences are not statistically significant. The average chronological ages for developmental stages D1, D2, D4, and D5 are 4.83, 13.84, 26.18, and 42.22 months, respectively. No data are available for D3 or D6, but Fleagle and Schaffler (1982) state that the permanent canines are erupt by 54 months of age. Galliari (1985) reports gingival eruption

times from birth up to 30 months of age in captive *C. apella*. Male tufted capuchins are precocious in eruption of both deciduous and permanent dentitions relative to females. The average chronological ages for developmental stages D1, D2, D3, and D4 are 4.36, 13.75, 14.88, and 26.00 months, respectively. Because no significant sexual differences are present in the permanent dentition up to 30 months of age, it is assumed that this pattern holds for D5 and D6. It appears that the absolute ages assigned to the developmental stages are approximately the same for both sexes of each species; therefore, it is assumed that dental eruption patterns are equivalent between the sexes. However, interspecific age differences are present. It should be noted that 1) there is a margin of error associated with each average chronological age given above (Fleagle and Schaffler, 1982; Galliari, 1985), 2) some skeletal growth may continue in D6 since long bone epiphyses remain unfused at 5.5 years of age in both species (Jungers and Fleagle, 1980), 3) some cranial sutures may remain open after eruption of the permanent dentition (Schultz, 1960), and 4) body weight may increase after eruption of the permanent dentition (Leigh, 1992). Some controversy exists over age of attainment of adult body weight (for discussion see Masterson, 1996).

Cranial variables

Twenty-three linear variables were measured on each skull with a helios caliper to the nearest 0.01 mm. The measurements are defined in Appendix 1. An analysis of

measurement repeatability reveals that the average measurement error was 0.733% for the cranial variables (Masterson, 1996).

Statistical methods

Ontogenetic patterns of cranial sexual dimorphism and interspecific comparisons of cranial form were investigated by means of univariate, bivariate, and multivariate statistics. Sexual differences in male and female developmental age group means were assessed by Student's *t*-test. The two-tailed hypothesis was used to examine levels of significance for differences in the unpaired *t*-values. Greene's (1989) *t*-test was used to examine the significance of interspecific differences in degree of adult cranial sexual dimorphism between the two species. Konigsberg's (1991) multivariate test of sexual dimorphism between populations was also performed.

The null hypothesis of ontogenetic scaling, where the sexes (or species) lie along the same ontogenetic continuum, was tested using bivariate growth allometries. Bivariate growth allometries of each sex and species (sexes pooled) were obtained by performing reduced major axis (RMA) regression on log-transformed data (similar results were found using least squares regression; therefore, only RMA results will be reported [for details see Masterson, 1996]). Basicranial length was chosen as the independent variable because it represents a good measure of overall skull size (Shea, 1983a; Ravosa, 1991a, 1992; Masterson and Leutenegger, 1992; Ravosa and Ross, 1994). Sex and species differences in RMA slopes were tested following Clarke (1980). The testing of RMA position differences followed Tsutakawa and Hewitt's (1977) "quick test" technique. For purpose of comparison, a nondimorphic ancestor was reconstructed such that the growth allometries were similar to modern females for the intersexual analyses and *C. albifrons* for the interspecific analyses. Patterns of dimorphism were interpreted from these conditions.

The underlying heterochronic processes were examined following the technique reviewed by Godfrey and Sutherland (1995a, b, 1996). In order to analyze sexual dimorphism in terms of heterochrony, data on

sexual differences in size and shape as well as the degree of sexual bimaturism are necessary. The growth allometries reported below provide the data on sexual differences in size and shape. Information on body weight growth, duration of ontogeny, timing of sexual maturity, and timing of growth spurts was used to assess the degree of sexual bimaturism (for discussion see Shea, 1986; Corner and Richtsmeier, 1991). For example, a lack of sexual bimaturism suggests that rate hypermorphosis, males growing at a faster rate than females but for the same length of time, underlies the observed pattern of ontogenetic scaling. Strong sexual bimaturism suggests that time hypermorphosis, males growing at the same rate as females but for a longer length of time, is responsible for this pattern. It is possible that the two processes may act in conjunction or at different times of development within an individual (Ravosa and Ross, 1994). A review of available *Cebus* life history data can be found in Masterson (1996).

Principal components analysis (PCA) was performed on both log size-and-shape (logged raw) and log shape (size-adjusted) data. The log size-and-shape PCA is the same as the multivariate generalization of allometry proposed by Jolicoeur (1963a, b). This technique provides a method to assess allometric and nonallometric scores for each developmental stage. Detailed discussion of the application of this technique can be found in Masterson and Leutenegger (1990). Unpaired *t*-tests were performed on each age group with sex as the factor to determine if significant ($P \leq 0.05$) sexual differences in PCA scores are present along axes I and II for both species. The second PCA was run following the technique developed to study size and shape by Darroch and Mosimann (1985). Detailed discussion of the application of this technique can be found in Jungers et al. (1988) or Falsetti et al. (1993). Unpaired *t*-tests were not performed on these age groups because this study is not examining "size" and "shape" alone (e.g., Falsetti et al., 1993). What is relevant to this study is the extent to which differences can be attributed to log shape vs. log size and shape in each species. This was examined by comparing the total variance accounted for by the log

TABLE 2. *T* values and significance levels for sex differences in developmental age group means in *Cebus albifrons*¹

Variables	D1	D3	D4	D5	D6
Palate width at canine	-0.153	1.631	2.645*	3.046**	9.705***
Palate width posterior to canine	-0.289	1.590	1.049	2.318*	4.976***
Palate length	0.004	0.645	1.043	1.978	4.578***
Lower facial length	0.605	1.398	0.651	2.582*	6.866***
Alveolar height	-0.731	0.532	0.244	-0.634	3.407***
Bimaxillary width	-0.174	1.601	2.083*	2.667*	8.365***
Biorbital width	0.227	1.331	-0.353	2.085*	4.980***
Interorbital width	1.016	-0.675	1.365	1.640	4.448***
Orbital width	0.211	1.691	0.282	1.733	4.491***
Orbital height	-0.206	0.750	1.090	1.719	2.327*
Postorbital constriction	-0.077	0.174	-0.840	2.226*	2.090*
Bizygomatic breadth	0.645	1.375	1.185	2.973**	9.576***
Anterior basicranial width	0.382	0.498	1.883	1.999	5.242***
Basioccipital length	-0.902	1.446	-0.164	2.684*	6.368***
Biauricular width	1.970	1.200	0.637	2.421*	4.393***
Bimastoid width	0.630	0.939	1.027	2.238*	6.466***
Vault height	-0.113	0.680	0.957	0.557	4.570***
Maximum cranial length	0.236	1.378	0.660	1.860	6.062***
Minimum cranial length	0.610	0.461	0.224	1.158	6.262***
Basicranial length	0.136	0.844	0.998	4.186***	8.346***
Basion-prosthion	0.286	1.311	0.570	3.013**	8.484***
Nasion-prosthion	-0.394	-1.016	3.066*	2.586*	4.663***
Neurocranial breadth	0.609	-1.808	-0.131	0.868	3.046**

¹ There are no specimens representing developmental stage D2.

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

shape PCA to the total variance of the log size-and-shape PCA. This information was then compared between the species to estimate the proportions of size-related shape differences.

Discriminant function analysis (DFA), also known as canonical variates analysis, was used to examine interspecific cranial form in multivariate space. The two species were broken down by sex, and the DFA was run on these ontogenetic samples (four groups). Detailed discussion of the application of this technique can be found in Albrecht (1980) or Klecka (1980).

All analyses were performed using the statistical package Systat version 5.2 (Wilkinson, 1992), except for Clarke's (1980) test of reduced major axes and Greene's (1989) *t*-test for interspecific differences in sexual dimorphism. Programs for these tests were written using ClarisWorks, version 3.1 (Claris, 1994).

RESULTS

Intersexual comparisons

Univariate analyses. Unpaired *t*-values and levels of significance for the 23 cranial variables are presented in Tables 2 and 3 for *C. albifrons* and *C. apella*, respectively. Means and standard errors for the sexes of

both species are presented in Masterson (1996). In *C. albifrons*, the univariate analyses (Table 2) indicate that the sexes are very similar in linear distance in the infant stage (D1). In all developmental stages, male means tend to be larger than their female counterparts. Females do possess larger means in several variables of developmental stages D1–D5, but in no case does the difference reach statistical significance. No significant sexual differences ($P \leq 0.05$) are present until the late-juvenile stage (D4) when significant sexual differences favoring males exist in palate width (palate width at canine), facial width (bimaxillary width), and facial height (nasion-prosthion). In the sub-adult stage (D5), a distinct pattern emerges in which significant sexual differences are present in variables associated with 1) the dental arcade (palate width at canine, palate width posterior to canine) and associated masticatory apparatus (bimaxillary width, postorbital constriction, bizygomatic breadth), 2) the lower viscerocranium associated with prognathism (lower facial length, basion-prosthion), 3) the neurocranium (basioccipital length, biauricular width, bimastoid width, basicranial length), and 4) facial height (nasion-prosthion) and width (biorbital width). All variables possess a strong

TABLE 3. *T* values and significance levels for sex differences in developmental age group means in *Cebus apella*

Variables	D1	D2	D3	D4	D5	D6
Palate width at canine	0.481	0.830	1.512	3.841***	5.136***	14.328***
Palate width posterior to canine	0.503	-0.587	1.656	3.087**	3.759***	8.492***
Palate length	-0.197	-0.733	1.161	3.758***	3.821***	12.193***
Lower facial length	0.334	0.613	1.701	4.059***	4.319***	11.986***
Alveolar height	-0.231	0.969	0.761	1.349	0.680	3.301**
Bimaxillary width	-0.209	-0.409	1.713	3.180**	3.172**	11.502***
Biorbital width	0.320	0.518	1.511	2.420*	3.079**	8.418***
Interorbital width	0.845	1.611	1.629	2.085*	2.310*	8.748***
Orbital width	0.826	-1.386	1.514	2.124*	1.760	4.712***
Orbital height	-0.901	0.384	1.982	1.847	0.720	1.127
Postorbital constriction	2.373*	0.508	2.736**	2.877**	4.080***	4.871***
Bizygomatic breadth	0.228	-0.011	1.654	3.632***	4.213***	13.145***
Anterior basicranial width	-0.389	1.965	1.896	3.206**	3.614***	6.796***
Basioccipital length	-0.713	0.117	1.278	1.136	1.858	6.977***
Biauricular width	0.160	0.613	2.863**	5.120***	4.914***	6.322***
Bimastoid width	0.227	1.440	2.278*	5.005***	4.137***	8.520***
Vault height	-0.179	0.059	1.524	1.538	3.602***	9.041***
Maximum cranial length	0.274	0.484	1.374	2.917**	3.530***	11.395***
Minimum cranial length	1.731	0.335	1.640	2.143*	3.417***	7.901***
Basicranial length	0.092	-0.368	2.076*	2.547*	4.122***	11.182***
Basion-prosthion	0.373	0.545	1.838	3.548***	4.139***	12.108***
Nasion-prosthion	-0.488	-1.832	1.835	1.908	2.471*	6.045***
Neurocranial breadth	0.348	1.807	1.606	2.622*	2.700**	4.645***

* $P \leq 0.05$.** $P \leq 0.01$.*** $P \leq 0.001$.

degree of sexual dimorphism in the mature adult stage (D6), as indicated by both unpaired *t*-tests and indices of cranial sexual dimorphism (Table 4). There does not appear to be an adolescent growth spurt present in females as observed in many highly dimorphic catarrhines (e.g., Shea, 1985a).

In *C. apella* (Table 3), the univariate analyses indicate that the sexes are very similar in linear distance in the infant and early-juvenile stages (D1, D2); however, male means tend to be larger than their female counterparts. Females do possess larger means in several variables of these two developmental stages, but in no case does the difference reach statistical significance. A significant sexual difference favoring males in postorbital constriction is present in D1 but not in D2. This finding may be an artifact of the small D2 sample because significant differences in postorbital constriction are present in all other developmental stage comparisons. No significant sexual differences are present in D2. Starting in D3 and continuing through D6, there is a strong tendency for an increase in both number and strength of significant sexual differences ($P \leq 0.05$), all favoring males.

A pattern of cranial sexual dimorphism emerges in the mid-juvenile stage (D3) in which the male neurocranium seems to be

TABLE 4. *Indices of cranial sexual dimorphism with interspecific differences*

Variables	<i>C. apella</i>	<i>C. albifrons</i>	Difference
Palate width at canine	1.163	1.122	0.041
Palate width posterior to canine	1.068	1.063	0.004
Palate length	1.113	1.076	0.037
Lower facial length	1.130	1.098	0.033
Alveolar height	1.096	1.125	-0.029
Bimaxillary width	1.151	1.117	0.033
Biorbital width	1.071	1.061	0.010
Interorbital width	1.232	1.128	0.104
Orbital width	1.043	1.057	-0.013
Orbital height	1.012	1.031	-0.019
Postorbital constriction	1.037	1.023	0.013
Bizygomatic breadth	1.172	1.118	0.054
Anterior basicranial width	1.073	1.061	0.012
Basioccipital length	1.127	1.104	0.023
Biauricular width	1.062	1.055	0.006
Bimastoid width	1.078	1.069	0.009
Vault height	1.068	1.038	0.030
Maximum cranial length	1.083	1.067	0.016
Minimum cranial length	1.063	1.050	0.013
Basicranial length	1.106	1.087	0.019
Basion-prosthion	1.130	1.114	0.016
Nasion-prosthion	1.073	1.081	-0.008
Neurocranial breadth	1.029	1.028	0.002

significantly larger along a mediolateral axis (postorbital constriction, biauricular width, bimastoid width) as well as along a midsagittal axis (basicranial length). Starting in

the late-juvenile stage (D4), there is a strong tendency for significant sexual differences to be present in variables related to four cranial regions: 1) the dental arcade (palate width at canine, palate width posterior to canine, palate length) and associated masticatory apparatus (bimaxillary width, postorbital constriction, bizygomatic breadth), 2) the lower viscerocranium associated with prognathism (lower facial length, maximum cranial length, basion-prosthion), 3) the neurocranium (anterior basicranial width, biauricular width, bimastoid width, minimum cranial length, basicranial length, neurocranial breadth), and 4) the orbital region (biorbital width, interorbital width, orbital width). Significant sexual differences in these regions continue to be present throughout the subadult and mature adult stages (D5, D6). Strong sexual dimorphism exists in the mature adult stage (D6) in all variables except orbital height. Indices of adult sexual dimorphism (Table 4) corroborate this finding. As in *C. albifrons*, a female adolescent growth spurt is not present.

Bivariate analyses. Growth allometries for the 22 cranial variables each regressed against basicranial length are listed in Tables 5 and 6 for *C. albifrons* and *C. apella*, respectively. All regressions are significant at the 5% level except for neurocranial breadth in female *C. albifrons*; therefore, this variable will not be included in the present analysis. Regression coefficients for the sexes of both species range from strong negative allometry for most variables of the neurocranium to strong positive allometry for most variables of the viscerocranium. In *C. albifrons* (Table 5), three distinct patterns emerge from these analyses. A marked pattern of ontogenetic scaling (Fig. 1) is present in 12 of 21 variables. These variables relate to four cranial regions: 1) the neurocranium directly associated with brain size (anterior basicranial width, biauricular width, bimastoid width, minimum cranial length), 2) the dental arcade associated with food processing functions (palate width at canine, palate width posterior to canine), 3) the lower viscerocranium associated with prognathism (lower facial length, maximum cranial length, basion-prosthion), and 4) fa-

cial height (nasion-prosthion) and width (bimaxillary width, biorbital width). In each case, male and female slopes are not significantly different at or below the 5% level of significance. The sexes are scaled versions of each other with no dissociation between size and shape as predicted by the null hypothesis of ontogenetic scaling.

The second pattern represents the five variables that possess significant ($P \leq 0.05$) position differences. Males are vertically transposed below the female line in basioccipital length. Males are transposed above the female line in palate length, orbital height, postorbital constriction, and vault height.

The third pattern represents the four variables that depart from ontogenetic scaling: alveolar height, interorbital width, orbital width, and bizygomatic breadth. Significantly different slopes indicate that size and shape are dissociated between the sexes. Males possess a significantly steeper positive slope in bizygomatic breadth (Fig. 2). In alveolar height (Fig. 3) and interorbital width, males possess significantly less steeper positive slopes, whereas males possess a significantly more negative slope in orbital width.

Growth allometries for *C. apella* (Table 6) indicate that three distinct patterns emerge from these analyses as well. First, ontogenetic scaling (Fig. 4) is present in eight variables that relate to four cranial regions: 1) the neurocranium directly associated with brain size (anterior basicranial width, vault height), 2) the dental arcade associated with food processing functions (palate width posterior to canine, palate length), 3) the lower viscerocranium associated with prognathism (lower facial length, maximum cranial length, basion-prosthion), and 4) facial width (biorbital width). As predicted by the null hypothesis, the sexes are scaled versions of each other with no dissociation between size and shape.

The second pattern represents the five variables that possess significant ($P \leq 0.05$) position differences: biauricular width, bimastoid width, minimum cranial length, nasion-prosthion, and neurocranial breadth. In all cases, males are vertically transposed above the female line.

TABLE 5. Allometric coefficients of various *Cebus albifrons* cranial variables regressed against basicranial length, including tests for sex differences in slope and position¹

Variables	Sex	N	Y int	Slope	95% C.I.	r	Sex differences	
							Slope	Position
Palate width at canine	M	85	-0.435	1.059	(0.951, 1.167)	0.891	NS	NS
	F	81	-0.404	1.035	(0.899, 1.169)	0.843		
Palate width posterior to canine	M	86	0.161	0.747	(0.673, 0.820)	0.897	NS	NS
	F	81	0.074	0.800	(0.688, 0.912)	0.809		
Palate length	M	84	-0.770	1.294	(1.202, 1.386)	0.947	NS	0.01
	F	79	-0.862	1.355	(1.198, 1.512)	0.874		
Lower facial length	M	85	-0.455	1.225	(1.152, 1.299)	0.962	NS	NS
	F	81	-0.567	1.293	(1.181, 1.405)	0.929		
Alveolar height	M	83	-0.368	2.529	(2.190, 2.867)	0.816	0.001	NT
	F	81	-0.459	3.094	(2.585, 3.604)	0.734		
Bimaxillary width	M	82	-0.415	1.197	(1.099, 1.296)	0.932	NS	NS
	F	82	-0.343	1.152	(1.010, 1.297)	0.854		
Biorbital width	M	84	0.016	0.924	(0.840, 1.007)	0.915	NS	NS
	F	80	0.024	0.923	(0.799, 1.047)	0.862		
Interorbital width	M	86	-2.602	1.906	(1.605, 2.208)	0.733	0.01	NT
	F	79	-3.203	2.267	(1.857, 2.677)	0.687		
Orbital width	M	86	-0.074	0.789	(0.707, 0.870)	0.886	0.05	NT
	F	82	-0.413	0.991	(0.843, 1.140)	0.771		
Orbital height	M	86	-0.723	0.798	(0.666, 0.929)	0.711	NS	0.01
	F	82	-0.726	0.803	(0.651, 0.956)	0.642		
Postorbital constriction	M	86	0.632	0.559	(0.464, 0.654)	0.691	NS	0.05
	F	81	0.372	0.717	(0.582, 0.851)	0.653		
Bizygomatic breadth	M	81	-0.327	1.215	(1.136, 1.295)	0.957	0.05	NT
	F	79	-0.122	1.095	(0.994, 1.195)	0.927		
Anterior basicranial width	M	82	0.423	0.700	(0.615, 0.783)	0.854	NS	NS
	F	80	0.303	0.771	(0.646, 0.896)	0.760		
Basioccipital length	M	85	-1.291	1.397	(1.305, 1.490)	0.954	NS	0.05
	F	82	-1.185	1.341	(1.179, 1.502)	0.849		
Biauricular width	M	84	0.384	0.719	(0.634, 0.805)	0.853	NS	NS
	F	80	0.194	0.832	(0.699, 0.956)	0.765		
Bimastoid width	M	82	0.497	0.702	(0.631, 0.772)	0.897	NS	NS
	F	78	0.428	0.741	(0.623, 0.859)	0.763		
Vault height	M	84	0.573	0.641	(0.571, 0.710)	0.878	NS	0.05
	F	79	0.346	0.779	(0.667, 0.890)	0.807		
Maximum cranial length	M	82	0.664	0.746	(0.686, 0.806)	0.933	NS	NS
	F	81	0.609	0.779	(0.690, 0.869)	0.877		
Minimum cranial length	M	81	1.008	0.488	(0.432, 0.544)	0.869	NS	NS
	F	81	0.847	0.583	(0.486, 0.681)	0.737		
Basion-prosthion	M	86	-0.431	1.272	(1.212, 1.331)	0.976	NS	NS
	F	82	-0.464	1.292	(1.201, 1.382)	0.954		
Nasion-prosthion	M	84	-0.394	1.096	(0.946, 1.246)	0.806	NS	NS
	F	81	-0.720	1.287	(1.103, 1.471)	0.804		
Neurocranial breadth	M	83	1.117	0.348	(0.264, 0.432)	0.396	NS	NS
	F	81	0.691	0.600	(0.423, 0.776)	0.170		

¹ M, male; F, female; N, sample size; Y int, Y intercept; Slope, reduced major axis (RMA) slope; 95% C.I., 95% confidence interval for RMA slope estimate; r, correlation coefficient; NS, not significant at $P \leq 0.05$; NT, not tested.

The third growth pattern represents the nine variables that depart from ontogenetic scaling: palate width at canine, alveolar height, bimaxillary width, interorbital width, orbital width, orbital height, postorbital constriction, bizygomatic breadth, and basioccipital length. Males possess significantly steeper positive slopes in palate width at canine, bimaxillary width, and bizygomatic breadth (Fig. 5). Males possess significantly less steeper positive slopes in alveolar height (Fig. 6), interorbital width, and basioccipital length. Males possess significantly more

negative slopes in orbital width, orbital height, and postorbital constriction.

Multivariate analyses. Results of the log size-and-shape PCAs for *C. albifrons* and *C. apella* are presented in Tables 7 and 8, respectively. The mean score for each developmental stage by sex is illustrated in Figures 7 and 8. Developmental stage D2 is not included in Figures 7 and 9 because no females represent this age group. In *C. albifrons*, principal component I accounts for 75.78% of the total sample variance. It

TABLE 6. Allometric coefficients of various *Cebus apella* cranial variables regressed against basicranial length, including tests for sex differences in slope and position¹

Variables	Sex	N	Y int	Slope	95% C.I.	r	Sex differences	
							Slope	Position
Palate width at canine	M	204	-0.597	1.165	(1.117, 1.212)	0.957	0.01	NT
	F	132	-0.445	1.070	(0.991, 1.148)	0.910		
Palate width posterior to canine	M	205	0.062	0.814	(0.769, 0.859)	0.921	NS	NS
	F	133	-0.093	0.905	(0.826, 0.984)	0.872		
Palate length	M	202	-0.589	1.193	(1.134, 1.252)	0.938	NS	NS
	F	132	-0.541	1.166	(1.075, 1.257)	0.898		
Lower facial length	M	206	-0.506	1.262	(1.218, 1.306)	0.968	NS	NS
	F	131	-0.561	1.295	(1.220, 1.370)	0.944		
Alveolar height	M	202	-3.516	2.444	(2.247, 2.640)	0.834	0.001	NT
	F	133	-5.208	3.457	(3.063, 3.852)	0.782		
Bimaxillary width	M	195	-0.551	1.300	(1.247, 1.353)	0.959	0.001	NT
	F	128	-0.323	1.164	(1.088, 1.241)	0.930		
Biorbital width	M	200	0.206	0.806	(0.765, 0.846)	0.935	NS	NS
	F	132	0.061	0.892	(0.812, 0.971)	0.868		
Interorbital width	M	204	-2.144	1.644	(1.515, 1.773)	0.839	0.01	NT
	F	133	-2.593	1.901	(1.621, 2.180)	0.638		
Orbital width	M	204	0.040	0.718	(0.670, 0.765)	0.886	0.05	NT
	F	134	0.159	0.837	(0.752, 0.923)	0.823		
Orbital height	M	206	0.145	0.669	(0.604, 0.734)	0.753	0.05	NT
	F	134	-0.091	0.815	(0.717, 0.913)	0.755		
Postorbital constriction	M	205	0.770	0.472	(0.424, 0.509)	0.835	0.05	NT
	F	134	0.548	0.601	(0.539, 0.663)	0.820		
Bizygomatic breadth	M	193	-0.468	1.307	(1.266, 1.348)	0.976	0.001	NT
	F	130	-0.192	1.142	(1.077, 1.207)	0.947		
Anterior basicranial width	M	200	0.417	0.706	(0.636, 0.776)	0.904	NS	NS
	F	130	0.405	0.712	(0.646, 0.779)	0.855		
Basioccipital length	M	205	-1.132	1.301	(1.195, 1.407)	0.964	0.01	NT
	F	134	-1.314	1.412	(1.310, 1.515)	0.911		
Biauricular width	M	197	0.540	0.628	(0.566, 0.690)	0.915	NS	0.01
	F	131	0.429	0.689	(0.628, 0.751)	0.866		
Bimastoid width	M	199	0.533	0.681	(0.619, 0.743)	0.938	NS	0.001
	F	132	0.524	0.683	(0.629, 0.736)	0.897		
Vault height	M	203	0.625	0.618	(0.582, 0.653)	0.915	NS	NS
	F	131	0.675	0.588	(0.533, 0.643)	0.855		
Maximum cranial length	M	204	0.679	0.740	(0.712, 0.767)	0.963	NS	NS
	F	134	0.639	0.762	(0.705, 0.819)	0.904		
Minimum cranial length	M	203	1.023	0.480	(0.452, 0.508)	0.911	NS	0.01
	F	131	0.895	0.553	(0.502, 0.603)	0.860		
Basion-prosthion	M	206	-0.492	1.311	(1.275, 1.348)	0.980	NS	NS
	F	133	-0.539	1.340	(1.277, 1.403)	0.963		
Nasion-prosthion	M	204	-0.535	1.196	(1.121, 1.271)	0.898	NS	0.01
	F	129	-0.626	1.257	(1.143, 1.370)	0.868		
Neurocranial breadth	M	200	1.197	0.305	(0.261, 0.349)	0.459	NS	0.05
	F	130	0.949	0.447	(0.365, 0.528)	0.439		

¹ M, male; F, female; N, sample size; Y int, Y intercept; slope, reduced major axis (RMA) slope; 95% C.I., 95% confidence interval for RMA slope estimate; r, correlation coefficient; NS, not significant at $P \leq 0.05$; NT, not tested.

distributes the skulls according to overall size, as evidenced by being significantly correlated with log size ($r = 0.965$; $P \leq 0.0001$). Males possess the larger score per developmental stage. Some degree of sexual dimorphism along component I is present in the mid-juvenile stage (D3) and progressively increases through the mature adult stage (D6), mimicking the results of the univariate analyses. Unpaired t -tests corroborate these findings in that significant sexual differences exist in PCA scores in D5

and D6. The variable loadings of component I are all positive, although a wide range of values does exist indicating that each variable contributes unequally to the first component. The first component loadings are interpreted as an "allometry vector" (Hursh, 1975; Shea, 1985b) because it shows the direction of size increase along with shape changes that occur in each variable.

Principal component II explains 8.44% of the remaining variance. The largest degree of sexual differentiation along component II

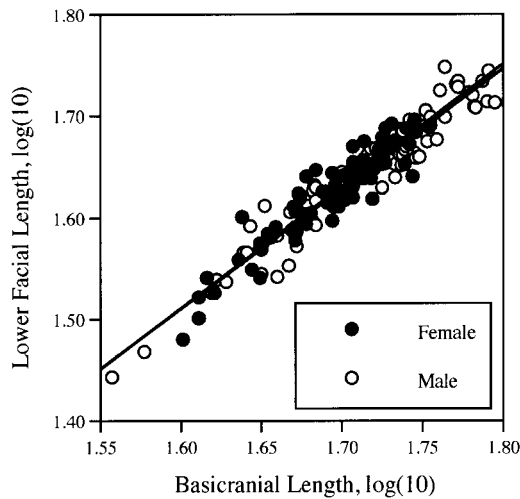


Fig. 1. An example of ontogenetic scaling in *C. albifrons*. Rate hypermorphosis is suggested as underlying this pattern.

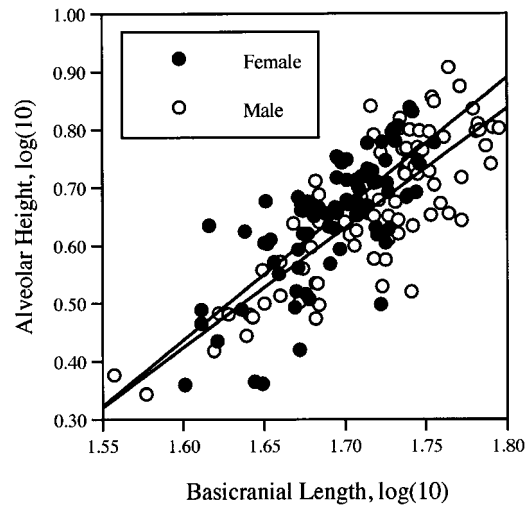


Fig. 3. An example of a departure from ontogenetic scaling in *C. albifrons*. An ancestral positive slope gets significantly less positive in alveolar height, suggesting males are paedomorphic via neoteny.

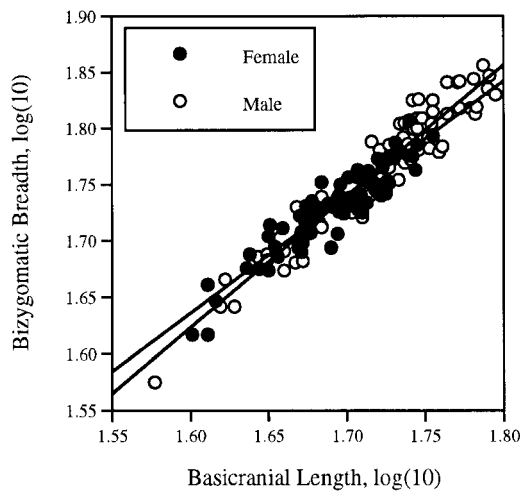


Fig. 2. An example of a departure from ontogenetic scaling in *C. albifrons*. An ancestral positive slope gets significantly more positive in bizygomatic breadth, suggesting males are peramorphic via acceleration.

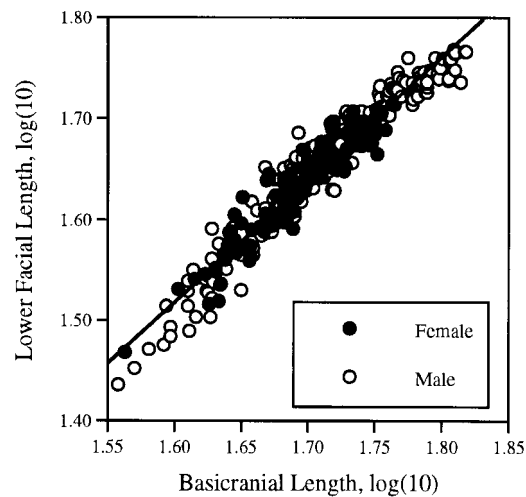


Fig. 4. An example of ontogenetic scaling in *C. apella*. Rate hypermorphosis is suggested as underlying this pattern.

occurs within the infant (D1) and subadult (D5) stages. A moderate influence in sexual differentiation occurs in the mid-juvenile and adult stages (D3, D6). The late-juvenile stage (D4) possesses the smallest degree of sexual differentiation. Unpaired *t*-tests indicate significant sexual differences exist in PCA scores in D5 and D6. Given the moderate to strong influence of component II in the

sexual differentiation of D1 and D3, the lack of significant sexual differences is likely due to small sample size for these age groups. Principal component II seems to represent nonallometric shape change because it possesses numerous bipolar component loadings and is not significantly correlated with log size ($r = 0.0615$; $P = 0.469$). The separation of the sexes by shape differences relates

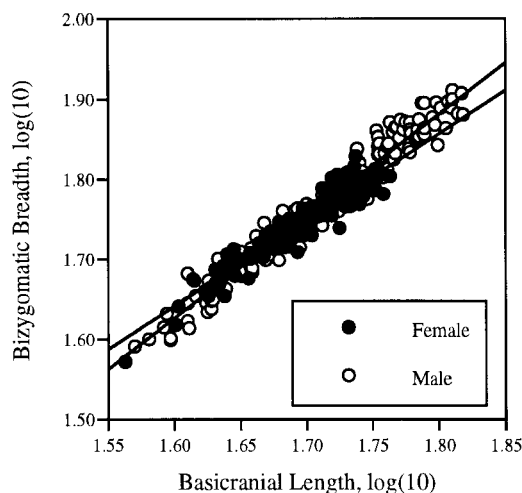


Fig. 5. An example of a departure from ontogenetic scaling in *C. apella*. An ancestral positive slope gets significantly more positive in bizygomatic breadth, suggesting males are peramorphic via acceleration.

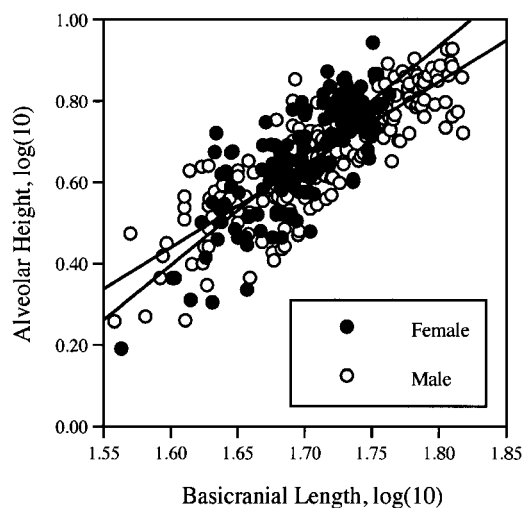


Fig. 6. An example of a departure from ontogenetic scaling in *C. apella*. An ancestral positive slope gets significantly less positive in alveolar height, suggesting males are paedomorphic via neoteny.

to variables possessing larger positive and negative loadings that either increase or decrease with respect to each other as one moves along the second component axis (Shea, 1983a, 1985b). Variables possessing strong positive loadings along component II are palate width at canine, interorbital width, bizygomatic breadth, basioccipital

length, basicranial length, and basion-prosthion. Variables possessing negative loadings are alveolar height, orbital width, orbital height, postorbital constriction, maximum cranial length, nasion-prosthion, and neurocranial breadth. These variables are primarily responsible for the separation of the sexes. Components I, II, and III (for discussion see Masterson, 1996) explain 90.30% of the total sample variance, with the final 9.70% being explained by the remaining 20 components.

In *C. apella*, principal component I accounts for 82.67% of the total sample variance and distributes the skulls according to overall size. Again, principal component I is significantly correlated with log size ($r = 0.995$; $P \leq 0.0001$). In both the infant and early-juvenile stages (D1, D2), the sexes possess approximately the same scores, although males are slightly larger. Starting in D3 and continuing through D6, males possess progressively larger component I scores. This indicates that some degree of sexual dimorphism has started in the mid-juvenile stage (D3) and continues through the mature adult stage (D6). As in *C. albifrons*, this mimics the results of the univariate analyses. Unpaired *t*-tests corroborate these findings; significant sexual differences in PCA scores are present in D3, D4, D5, and D6. The first component loadings are interpreted as an allometry vector.

Principal component II explains 7.40% of the remaining variance. A clear separation of the sexes along component II occurs within the infant stage (D1), only to decrease in importance in the early- and mid-juvenile stages (D2, D3). By the late-juvenile stage and continuing through the mature adult stage (D4, D5, D6), component II substantially increases its importance in the differentiation of the sexes. Unpaired *t*-tests indicate that only D6 possesses significant sexual differences in PCA scores. As in *C. albifrons*, component II seems to represent nonallometric shape change because it possesses bipolar loadings and is not significantly correlated with log size ($r = 0.083$; $P = 0.171$). Variables possessing strong positive loadings along component II are palate width at canine, bimaxillary width, interorbital width, bizygomatic breadth, and basion-prosthion.

TABLE 7. Variable loadings on the first three principal components for analyses of the pooled (log size-and-shape) and size-adjusted (log shape) *Cebus albifrons* samples

Variables	Log size-and-shape			Log shape		
	Factor I	Factor II	Factor III	LS I	LS II	LS III
Palate width at canine	0.2085	0.1196	0.1432	-0.0377	-0.0682	-0.0475
Palate width posterior to canine	0.1343	0.0229	0.1384	0.0923	0.0360	0.0798
Palate length	0.2452	0.0061	0.1882	-0.0997	0.0330	-0.1438
Lower facial length	0.2420	0.0453	0.1622	-0.0954	-0.0061	-0.0919
Alveolar height	0.4982	-0.7607	-0.5059	-0.7722	0.5277	0.3589
Bimaxillary width	0.2223	0.0577	0.1733	-0.0588	-0.0081	-0.0357
Biorbital width	0.1758	0.0275	0.0559	0.0088	0.0096	0.1556
Interorbital width	0.3328	0.7311	-0.5805	-0.3382	-0.7844	0.4169
Orbital width	0.1410	-0.0164	0.0948	0.0764	0.0666	0.1904
Orbital height	0.1019	-0.0311	0.2050	0.1640	0.1069	0.1138
Postorbital constriction	0.0721	-0.0224	0.1265	0.2128	0.0979	0.3492
Bizygomatic breadth	0.2315	0.0711	0.1001	-0.0850	-0.0358	0.0076
Anterior basicranial width	0.1222	0.0137	0.1627	0.1240	0.0568	0.1641
Basioccipital length	0.2541	0.1601	0.0014	-0.1420	-0.1433	0.0184
Biauricular width	0.1282	0.0072	0.1242	0.1098	0.0539	0.1998
Bimastoid width	0.1279	0.0147	0.1183	0.1061	0.0445	0.1875
Vault height	0.1087	0.0000	0.0872	0.1312	0.0565	0.2190
Maximum cranial length	0.1427	-0.0172	0.1301	0.0770	0.0719	0.1314
Minimum cranial length	0.0867	0.0144	0.0653	0.1707	0.0451	0.2842
Basicranial length	0.1959	0.0979	0.1005	-0.0172	-0.0522	0.0356
Basion-prosthion	0.2515	0.0869	0.1414	-0.1127	-0.0491	-0.0926
Nasion-prosthion	0.2044	-0.0793	0.2597	-0.0257	0.1300	-0.2249
Neurocranial breadth	0.0275	-0.0209	0.1153	0.2876	0.1050	0.3928
Total variance	0.7578	0.0844	0.0608	0.4692	0.1945	0.0849

TABLE 8. Variable loadings on the first three principal components for analyses of the pooled (log size-and-shape) and size-adjusted (log shape) *Cebus apella* samples

Variables	Log size-and-shape			Log shape		
	Factor I	Factor II	Factor III	LS I	LS II	LS III
Palate width at canine	0.2173	0.1214	0.0819	-0.0410	-0.1074	-0.1603
Palate width posterior to canine	0.1594	0.0959	0.1076	0.0623	-0.0007	-0.0398
Palate length	0.2284	0.0784	0.1353	-0.0726	-0.0665	-0.2088
Lower facial length	0.2559	0.0999	0.1441	-0.1081	-0.1061	-0.2198
Alveolar height	0.4904	-0.8347	-0.2181	-0.7843	0.4910	0.2882
Bimaxillary width	0.2435	0.1122	0.1044	-0.0932	-0.1266	-0.2326
Biorbital width	0.1553	0.0503	0.0091	0.0573	0.0316	0.0924
Interorbital width	0.3052	0.3951	-0.8469	-0.1869	-0.7300	0.6073
Orbital width	0.1311	0.0413	0.1249	0.1088	0.1114	0.0401
Orbital height	0.1104	0.0261	0.1168	0.1454	0.1520	0.1024
Postorbital constriction	0.0860	0.0361	0.0242	0.1811	0.1322	0.1932
Bizygomatic breadth	0.2412	0.1242	0.1026	-0.0836	-0.1341	-0.2109
Anterior basicranial width	0.1247	0.0841	0.1007	0.1262	0.0538	0.0302
Basioccipital length	0.2402	0.0970	0.0729	-0.1046	-0.1258	-0.2524
Biauricular width	0.1222	0.0814	0.1096	0.1315	0.0700	0.0621
Bimastoid width	0.1231	0.0749	0.1115	0.1217	0.0594	0.0307
Vault height	0.1072	0.0882	0.0607	0.1575	0.0808	0.0905
Maximum cranial length	0.1453	0.0757	0.0829	0.0840	0.0305	-0.0022
Minimum cranial length	0.0861	0.0739	0.0618	0.1900	0.1096	0.1066
Basicranial length	0.1917	0.0986	0.1123	-0.0053	-0.0409	-0.1433
Basion-prosthion	0.2609	0.1045	0.1104	-0.1244	-0.1394	-0.2529
Nasion-prosthion	0.2209	-0.0034	0.2144	-0.0648	0.0604	-0.1737
Neurocranial breadth	0.0282	0.0675	0.0368	0.2964	0.1986	0.2621
Total variance	0.8267	0.0740	0.0323	0.5951	0.1668	0.0662

Alveolar height and nasion-prosthion possess negative loadings. These variables are primarily responsible for the separation of the sexes. Components I, II, and III (see Masterson, 1996) explain 93.30% of the total

sample variance, with the final 6.70% being explained by the remaining 20 components.

Results of the log shape (LS) PCAs for *C. albifrons* and *C. apella* are presented in Tables 7 and 8, respectively. The mean score

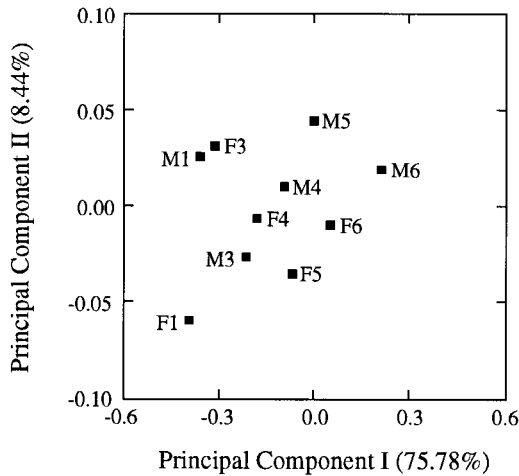


Fig. 7. Log size-and-shape PCA scores for *C. albifrons*. Average scores provided for each developmental stage. M, male; F, female. Numbers correspond to D1–D6 (no D2 shown).

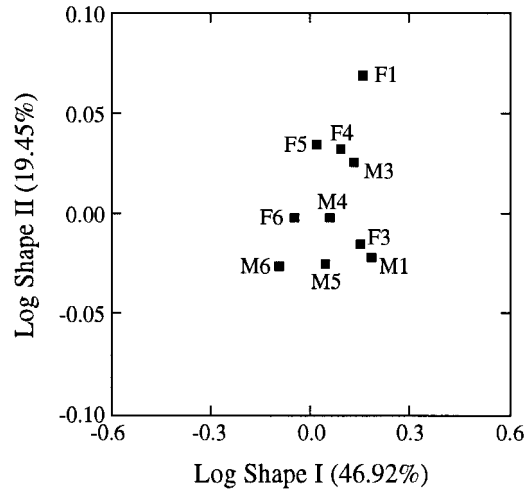


Fig. 9. Log shape PCA scores for *C. albifrons*. Average scores provided for each developmental stage. M, male; F, female. Numbers correspond to D1–D6 (no D2 shown).

for each developmental stage by sex is illustrated in Figures 9 and 10. In *C. albifrons*, LS I accounts for 46.92% of the total sample variance. After isometric size has been removed, LS I still separates the sexes by size, as evidenced by being significantly correlated with log size ($r = -0.788$; $P \leq 0.0001$). Log shape I possesses a wide range of loadings with almost equal numbers of positive (12 of 23 variables) and negative (11 of 23 variables) loadings. Females possess the

larger score in the mid-juvenile, late-juvenile, and adult stages (D3, D4, D6). Males possess the larger score in the infant and subadult stages (D1, D5).

Log shape II explains 19.45% of the remaining variance. Shape differences between the sexes are not significantly correlated with log size ($r = -0.107$; $P = 0.205$) along LS II. Females possess the larger score in all developmental stages except in the mid-juvenile stage (D3). Log shape II

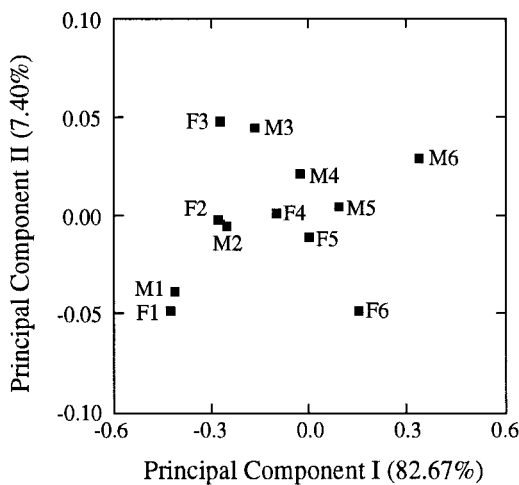


Fig. 8. Log size-and-shape PCA scores for *C. apella*. Average scores provided for each developmental stage. M, male; F, female. Numbers correspond to D1–D6.

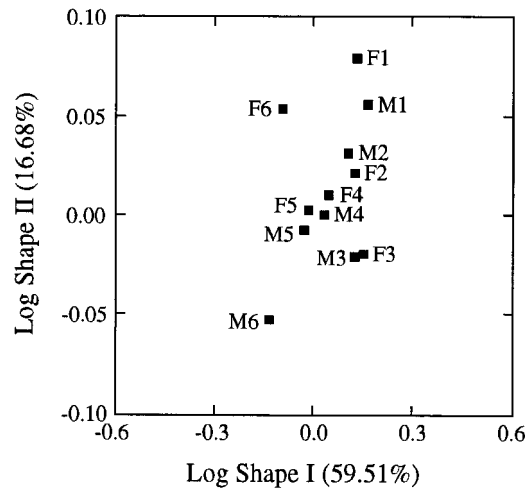


Fig. 10. Log shape PCA scores for *C. apella*. Average scores provided for each developmental stage. M, male; F, female. Numbers correspond to D1–D6.

seems to separate the sexes more than LS I. Log shape I, II, and III (see Masterson, 1996) explain 74.86% of the total sample variance, with the final 25.14% being explained by the remaining 20 components.

In *C. apella*, log shape I accounts for 59.51% of the total sample variance. As in *C. albifrons*, LS I still separates the sexes by size, as evidenced by being significantly correlated with log size ($r = -0.861$; $P \leq 0.0001$). Log shape I possesses a wide range of loadings with almost equal numbers of positive (12 of 23 variables) and negative (11 of 23 variables) loadings. Females possess the larger score in all developmental stages except in the infant stage.

Log shape II explains 16.68% of the remaining variance. Shape differences between the sexes are correlated to log size ($r = -0.323$; $P \leq 0.0001$), contrary to the results observed for *C. albifrons*. Females possess the larger score in all developmental stages. Log shape II seems to separate the sexes more than LS I, especially in the infant and mature adult stages (D1, D6). Log shape I, II, and III (see Masterson, 1996) explain 82.81% of the total sample variance, with the final 17.19% being explained by the remaining 20 components.

Interspecific comparisons

Univariate analyses. Table 9 provides Tg values and levels of significance for interspecific differences in degree of sexual dimorphism calculated using Greene's (1989) *t*-test. *Cebus apella* possesses significantly ($P \leq 0.05$) larger levels of sexual dimorphism in seven variables: palate width at canine, palate length, lower facial length, bimaxillary width, interorbital width, bizygomatic breadth, and vault height. Konigsberg's (1991) multivariate test reveals a significant interaction exists between sex and species (Wilks' lambda = 0.6939, $F = 2.4931$, $df = 23, 130$, $P = 0.0006$), indicating that overall levels of sexual dimorphism are significantly different between the species.

Bivariate analyses. Despite the presence of several significant sexual differences in slope values in each species, interspecific bivariate analyses were performed. Allometry coefficients are presented in Table 10.

TABLE 9. Tg values and significance levels for interspecific comparisons of sexual dimorphism between *C. albifrons* and *C. apella*¹

Variables	Tg values
Palate width at canine	3.091***
Palate width posterior to canine	0.707
Palate length	2.219*
Lower facial length	2.252*
Alveolar height	-0.271
Bimaxillary width	2.696**
Biorbital width	1.137
Interorbital width	2.586**
Orbital width	-0.828
Orbital height	-1.093
Postorbital constriction	0.995
Bizygomatic breadth	3.422***
Anterior basicranial width	1.031
Basioccipital length	0.882
Biauricular width	0.439
Bimastoid width	0.764
Vault height	2.822**
Maximum cranial length	1.421
Minimum cranial length	1.188
Basicranial length	1.602
Nasion-prosthion	1.444
Nasion-prosthion	0.113
Neurocranial breadth	0.200

¹ Positive scores indicate *C. apella* possesses a larger degree of sexual dimorphism than *C. albifrons*.

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

Regression coefficients for both species range from strong negative allometry for most variables of the neurocranium to strong positive allometry for most variables of the viscerocranium. All regressions are significant at the 5% level. Again, three distinct patterns emerge from these analyses. First, a pattern of interspecific ontogenetic scaling is present in seven of 22 cranial variables (Fig. 11): alveolar height, orbital height, basioccipital length, bimastoid width, maximum cranial length, minimum cranial length, and neurocranial breadth.

The second pattern represents the eight variables that possess significant ($P \leq 0.05$) position differences. *Cebus apella* is transposed below the *C. albifrons* line in palate width at canine, palate width posterior to canine, and lower facial length. *Cebus apella* is transposed above the *C. albifrons* line in postorbital constriction, anterior basicranial width, biauricular width, vault height, and nasion-prosthion.

The third pattern represents the seven variables in which the species depart from interspecific ontogenetic scaling. *Cebus apella* possesses a significantly steeper posi-

TABLE 10. Allometric coefficients of *Cebus albifrons* and *Cebus apella* cranial variables regressed against basicranial length, including tests for species differences in slope and position¹

Variables	Species	N	Y int	Slope	95% C.I.	r	Species differences	
							Slope	Position
Palate width at canine	AL	166	-0.541	1.118	(1.036, 1.199)	0.882	NS	0.001
	AP	336	-0.594	1.161	(1.120, 1.202)	0.946		
Palate width posterior to canine	AL	166	0.127	0.767	(0.704, 0.830)	0.874	NS	0.001
	AP	338	0.024	0.836	(0.798, 0.874)	0.910		
Palate length	AL	163	-0.780	1.315	(1.226, 1.404)	0.922	0.001	NT
	AP	334	-0.570	1.183	(1.135, 1.230)	0.930		
Lower facial length	AL	167	-0.473	1.236	(1.178, 1.295)	0.953	NS	0.001
	AP	337	-0.516	1.268	(1.231, 1.305)	0.963		
Alveolar height	AL	164	-3.960	2.707	(2.419, 2.994)	0.772	NS	NS
	AP	323	-3.912	2.682	(2.502, 2.863)	0.805		
Bimaxillary width	AL	164	-0.410	1.194	(1.117, 1.271)	0.914	0.05	NT
	AP	323	-0.502	1.271	(1.228, 1.314)	0.953		
Biorbital width	AL	164	-0.034	0.955	(0.887, 1.023)	0.895	0.001	NT
	AP	332	0.173	0.825	(0.789, 0.861)	0.919		
Interorbital width	AL	165	-2.817	2.034	(1.800, 2.269)	0.725	0.001	NT
	AP	337	-2.290	1.726	(1.606, 1.846)	0.791		
Orbital width	AL	168	-0.162	0.841	(0.769, 0.913)	0.845	0.05	NT
	AP	338	-0.001	0.742	(0.702, 0.783)	0.868		
Orbital height	AL	168	-0.042	0.782	(0.688, 0.876)	0.692	NS	NS
	AP	340	0.100	0.698	(0.644, 0.752)	0.740		
Postorbital constriction	AL	167	-0.571	0.597	(0.521, 0.673)	0.672	NS	0.001
	AP	339	0.705	0.509	(0.477, 0.541)	0.830		
Bizygomatic breadth	AL	160	-0.317	1.209	(1.140, 1.279)	0.951	0.01	NT
	AP	323	-0.415	1.275	(1.240, 1.310)	0.968		
Anterior basicranial width	AL	162	0.389	0.720	(0.650, 0.789)	0.833	NS	0.01
	AP	330	0.411	0.709	(0.674, 0.744)	0.895		
Basioccipital length	AL	167	-1.260	1.382	(1.298, 1.466)	0.921	NS	NS
	AP	339	-1.165	1.322	(1.277, 1.367)	0.950		
Biauricular width	AL	164	0.337	0.748	(0.681, 0.815)	0.831	NS	0.05
	AP	328	0.481	0.660	(0.629, 0.692)	0.901		
Bimastoid width	AL	160	0.473	0.715	(0.657, 0.774)	0.864	NS	NS
	AP	331	0.510	0.693	(0.664, 0.721)	0.927		
Vault height	AL	163	0.539	0.663	(0.606, 0.719)	0.848	NS	0.001
	AP	334	0.635	0.612	(0.583, 0.641)	0.904		
Maximum cranial length	AL	163	0.662	0.748	(0.701, 0.794)	0.920	NS	NS
	AP	338	0.664	0.748	(0.723, 0.773)	0.950		
Minimum cranial length	AL	162	0.955	0.519	(0.472, 0.566)	0.830	NS	NS
	AP	334	0.975	0.507	(0.482, 0.532)	0.897		
Basion-prosthion	AL	168	-0.424	1.268	(1.221, 1.315)	0.971	0.05	NT
	AP	339	-0.499	1.316	(1.285, 1.345)	0.977		
Nasion-prosthion	AL	165	-0.698	1.274	(1.158, 1.389)	0.820	NS	0.001
	AP	333	-0.536	1.199	(1.138, 1.261)	0.887		
Neurocranial breadth	AL	164	0.966	0.436	(0.358, 0.515)	0.313	NS	NS
	AP	330	1.106	0.357	(0.317, 0.396)	0.462		

¹ AL, *Cebus albifrons*; AP, *Cebus apella*; N, sample size; Y int, Y intercept; slope, reduced major axis (RMA) slope estimate; 95% C.I., 95% confidence interval for RMA slope estimate; r, correlation coefficient; NS, not significant at $P \leq 0.05$; NT, not tested.

tive slope in bimaxillary width, bizygomatic breadth (Fig. 12), and basion-prosthion. *Cebus apella* possesses a significantly less steeper positive slope in palate length (Fig. 13) and interorbital width. *Cebus apella* possesses a significantly more negative slope in biorbital width and orbital width.

Multivariate analyses. Results of the interspecific comparison between the log size-and-shape (*C. albifrons*: Fig. 7; *C. apella*: Fig. 8) and log shape (*C. albifrons*: Fig. 9; *C. apella*: Fig. 10) PCA scores reveals that 57.41% of *C. albifrons*' total sample variance

is explained by log size-and-shape, with the remaining 42.59% being explained by log shape. By contrast, 68.34% of *C. apella*'s total sample variance is explained by log size-and-shape, with the remaining 31.66% being explained by log shape. This suggests that size, rather than shape, plays a major role in distinguishing individuals of different age and sex in both species; however, size is more influential in *C. apella*.

Results of the interspecific DFA are presented in Table 11. Figure 14 displays 90% probability ellipsoids for each group's scores.

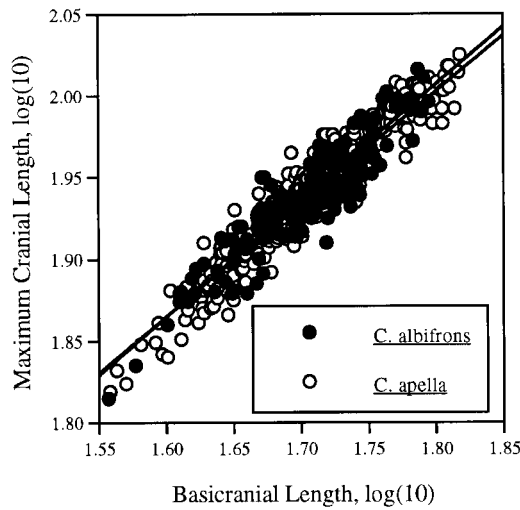


Fig. 11. An example of interspecific ontogenetic scaling. *Cebus apella* transcends the cranial form of *C. albifrons*.

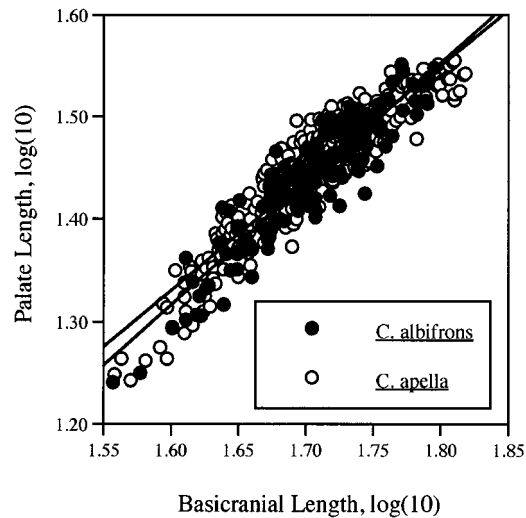


Fig. 13. An example of a departure from interspecific ontogenetic scaling. An ancestral positive slope gets significantly less positive in palate length, suggesting *C. apella* is paedomorphic via neoteny.

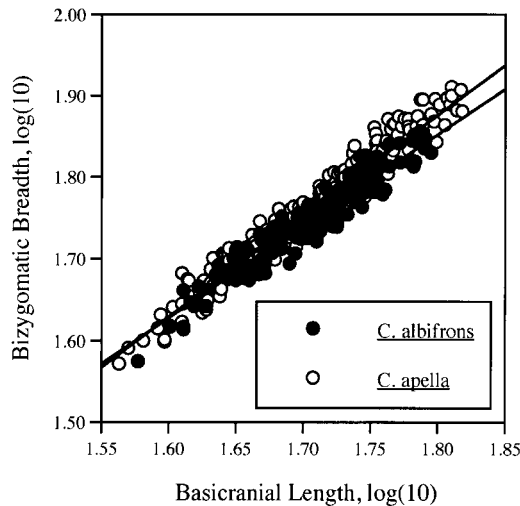


Fig. 12. An example of a departure from interspecific ontogenetic scaling. An ancestral positive slope gets significantly more positive in bizygomatic breadth, suggesting *C. apella* is peramorphic via acceleration.

The DFA is highly significant (Wilks' $\lambda = 0.1974$, $F = 12.1294$, $df = 69, 1159$, $P = 0.0000$). Thus, it is not surprising that function I is highly significant: $P = 0.0000$. Function I possesses a canonical correlation of 0.848; therefore, a high association exists between sex by species and function I. The two species as well as the sexes of *C. apella* are differentiated along function I. Variables possessing the largest discriminating power

TABLE 11. Canonical loadings, canonical correlations, and probabilities that sex by species differs from each other in the discriminant function analysis

Variables	Function I	Function II
Palate width at canine	-0.1055	0.5262
Palate width posterior to canine	-0.1134	0.3252
Palate length	-0.0149	0.2969
Lower facial length	-0.0435	0.3586
Alveolar height	-0.0185	0.0901
Bimaxillary width	-0.1911	0.3689
Biorbital width	0.1304	0.3286
Interorbital width	0.0141	0.4319
Orbital width	0.0799	0.2799
Orbital height	0.0394	0.1027
Postorbital constriction	0.2098	0.3481
Bizygomatic breadth	-0.0602	0.4053
Anterior basicranial width	-0.0261	0.4015
Basioccipital length	0.0473	0.2930
Biauricular width	0.0459	0.4389
Bimastoid width	0.0294	0.4727
Vault height	-0.0886	0.2609
Maximum cranial length	-0.0063	0.3850
Minimum cranial length	0.0330	0.4623
Basicranial length	0.0070	0.3736
Nasion-prosthion	-0.0274	0.3725
Nasion-prosthion	-0.1971	0.2340
Neurocranial breadth	-0.0376	0.3861
Canonical correlation	0.8483	0.4928
P	0.0000	0.0000

(loading > 0.1000) are palate width at canine, palate width posterior to canine, bimaxillary width, biorbital width, postorbital constriction, and nasion-prosthion. Variables

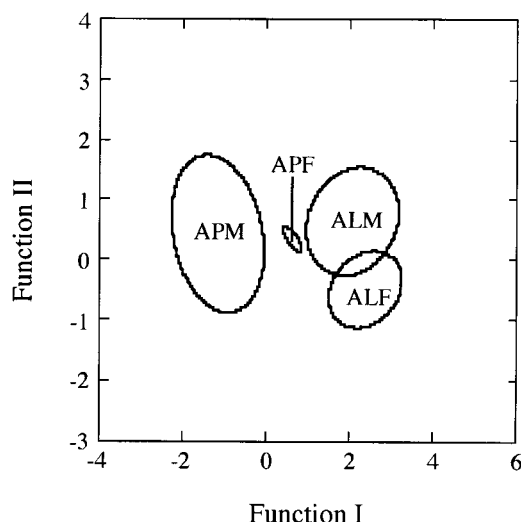


Fig. 14. Discriminant function I scores plotted against function II scores, showing 90% probability ellipsoids for each sex of both species. ALF, *C. albifrons* females; ALM, *C. albifrons* males; APF, *C. apella* females; APM, *C. apella* males.

possessing little discriminating power are alveolar height, interorbital width, anterior basicranial width, bimastroid width, maximum cranial length, basicranial length, and basion-prosthion. (Similar results were found in a DFA using species membership as the factor, but are not reported in the present study.)

Discriminant function II is also highly significant ($P = 0.0000$). It possesses a canonical correlation of 0.493. Function II differentiates the sexes of *C. albifrons* but plays no role in differentiating the sexes of *C. apella*. Variables possessing the largest discriminating power are palate width at canine, palate width posterior to canine, lower facial length, bimaxillary width, biorbital width, interorbital width, postorbital constriction, bizygomatic breadth, anterior basicranial width, biauricular width, bimastroid width, maximum cranial length, minimum cranial length, basicranial length, basion-prosthion, and neurocranial breadth.

DISCUSSION

Intersexual comparisons

Hypothesis 1 predicts that males of each species will possess larger means per cranial variable and be scaled-up versions of the females. Results of the univariate and bivari-

ate analyses corroborate this hypothesis. In *C. albifrons* (Table 2), significant sexual differences favoring males first emerge in the late-juvenile stage (D4), or at approximately 26.2 months of age. A distinct pattern of sexual dimorphism is present by the subadult stage (D5), approximately 42.2 months of age, in which all cranial regions except the orbits show significant sexual differences. This pattern continues into the adult stage (D6), which also includes significant sexual differences in the orbital region. These findings are similar to patterns present in *C. apella* (Table 3); however, several differences are present. In *C. apella*, significant sexual differences first emerge in the mid-juvenile stage (D3), or approximately 14.8 months of age, in four variables of the neurocranium. Starting in the late-juvenile stage (D4), approximately 26.0 months of age, a distinct pattern of sexual dimorphism is present in all cranial regions. Significant sexual differences in these regions continue to be present throughout the subadult and mature adult stages (D5, D6). These analyses suggest that 1) males of both species are growing at a faster rate per developmental stage than females, a finding that corroborates the results of Corner and Richtsmeier's (1991) analysis of *C. apella*, and 2) significant sexual dimorphism appears earlier in development in *C. apella*.

Bivariate growth allometries confirm that ontogenetic scaling occurs in both species' crania but not to the same degree as observed in other studies of primate craniofacial morphology (Shea, 1983a, 1992; Cochar, 1985; Cheverud and Richtsmeier, 1986; Leutenegger and Masterson, 1989b; Cole, 1990; Hays, 1990, 1991; Corner and Richtsmeier, 1991, 1992, 1993; Leigh and Cheverud, 1991; Ravosa, 1991a, b, 1992; Richtsmeier et al., 1993; Ravosa and Ross, 1994). In *C. albifrons*, ontogenetic scaling is present in 12 variables (Table 5; Fig. 1), whereas in *C. apella* ontogenetic scaling is present in only eight variables (Table 6; Fig. 4). In these variables, shape differences between the sexes can be interpreted as the result of an extension of relative growth from smaller females to larger overall size in males (Shea, 1986). Thus, males are peramorphic or transcend the female form (Alberch et al., 1979). The univariate results, in

conjunction with a lack of sexual bimaturism in each species (Masterson, 1996), suggest that the heterochronic process of rate hypermorphosis is the primary factor underlying the patterns of ontogenetic scaling present in *C. albifrons* and *C. apella*.

Departures from ontogenetic scaling suggest that other heterochronic processes are acting in both *C. albifrons* and *C. apella* as well. In *C. albifrons* (Table 5; Fig. 2), an ancestral positive slope for bizygomatic breadth gets significantly more positive, whereas an ancestral negative slope in orbital width gets significantly more negative. The heterochronic process of acceleration is suggested as underlying these findings. Ancestral patterns of allometry are dissociated and accelerated so that shape change progresses further and descendant adults are peramorphic in morphology (Shea, 1989). In alveolar height (Fig. 3) and interorbital width, an ancestral positive slope gets significantly less positive; therefore, the heterochronic process of neoteny is suggested as underlying these findings. In these two variables, males are paedomorphic or retain the ancestral juvenile shapes. Ancestral patterns of allometry are dissociated and retarded, revealing that shape change does not proceed as far and descendant adults are juvenilized in morphology (Shea, 1989). The departures in *C. albifrons* are associated with the mid-facial region (alveolar height, interorbital width, orbital width) and larger zygomatic arches (bizygomatic breadth) in males. The latter may be related to dietary and/or foraging differences between the sexes (see below).

In *C. apella* (Table 6; Fig. 5), an ancestral positive slope gets significantly more positive in palate width at canine, bimaxillary width, and bizygomatic breadth, whereas an ancestral negative slope gets significantly more negative in orbital width, orbital height, and postorbital constriction. The heterochronic process of acceleration is suggested as underlying these findings. In alveolar height (Fig. 6), interorbital width, and basioccipital length, an ancestral positive slope gets significantly less positive; therefore, the heterochronic process of neoteny is suggested as underlying these findings. The departures in *C. apella* seem to be associated with either the canine (palate width at

canine), orbital shape (interorbital width, orbital width, orbital height), the basicranium (basioccipital length), or increased robusticity due to its hard-object diet (bimaxillary width, postorbital constriction, and bizygomatic breadth).

Hypothesis 2 predicts that males will possess a different pattern of cranial variation in variables associated with mastication if ecological divergence has occurred. Results of the univariate and bivariate analyses provide some support for this hypothesis. Univariate analyses indicate that significant cranial variation occurs in the dental arcade and masticatory apparatus during ontogeny in males of both capuchin species. Stronger support for this hypothesis is revealed by the departures from ontogenetic scaling that are present in the masticatory apparatuses of both species.

In exploring possible Ceboid models for the evolution of the hominoid dentition, Kinzey (1974) concludes that the dentition of *C. apella* is adapted for powerful crushing of small, hard objects. Among the many morphological characteristics cited as correlates of hard-object feeding in *C. apella* are 1) a marked postorbital constriction that relates to a forwardly placed temporalis muscle and 2) widely flaring and robust zygomatic arches (Kinzey, 1974; Rosenberger and Kinzey, 1976; Cole, 1992). Although these features characterize *C. apella* as a species, it is likely that sexual differences exist, with males showing a stronger degree of the above characteristics compared to females. Indeed, this seems to be true given that strong sexual differences in means are present in variables directly related to the masticatory musculature (bimaxillary width, postorbital constriction, bizygomatic width). The nonallometric relationships of these variables, indicated by both growth allometries and PCA scores, may provide for larger infratemporal fossae to accommodate an increase in masseter and temporalis musculature. Cole (1992) reports significant sexual differences in all mandibular variables in his study, including infratemporal fossae size. Cole concludes that male tufted capuchins possess the ability to generate higher bite force as the result of both absolutely larger muscle size and greater mechanical advantage. Thus, some degree of

sexual dimorphism exists in the tufted capuchin's masticatory apparatus.

In *C. albifrons*, the dissociation of size and shape in bizygomatic breadth suggests that some degree of dietary differences may exist between the sexes in this species as well. Cole (1992) reports similar results for mandibular sex differences in *C. albifrons* as present in *C. apella*. Because males possess both significantly wider, flaring zygomatic arches and larger infratemporal fossae, some degree of sexual dimorphism exists in the white-fronted capuchin's masticatory apparatus.

Although general diet composition is known for both species (e.g., Terborgh, 1983; Robinson and Janson, 1987; Janson and Boinski, 1992), little data exists pertaining to the presence of significant sexual differences in diet and foraging strategies. Males of both species possess larger infratemporal fossae, which in turn allow for larger masticatory musculature. One would predict that this characteristic may be needed for the opening of hard-object foodstuffs such as *Astrocaryum* nuts. This does not seem to be the case. In *C. apella*, Terborgh (1983:84) reports that "half-grown juveniles seemed no less capable of this than adults," whereas *C. albifrons* cannot open the nuts using their teeth at any developmental stage without the help of beetles first softening the outer coating. Although there may be other unknown sexual differences in diet, this finding suggests that sexual differences may be present in foraging strategies in these two capuchin species. Indeed, Janson and Boinski (1992) suggest that foraging differences are present in *C. apella*, with adult males foraging in larger diameter substrates. This behavior is likely an outcome of overall larger adult male size and their larger masticatory musculature. No data are known regarding sexual differences in foraging strategies in *C. albifrons*. Until more detailed data on sexual differences in diet and foraging strategies are available, the selective forces underlying the observed differences in trophic structures cannot be said with certainty. It may be that females prefer males with wider faces (cheek bones), which in turn allow the males the ability to generate higher bite force.

The underlying selective regime that best explains the majority of the observed patterns of cranial sexual dimorphism in each species is sexual selection. Available data pertaining to the behavioral ecology of these species (Defler, 1979a, b, 1982; Izawa, 1980; Freese and Oppenheimer, 1981; Terborgh, 1983; Janson, 1984, 1986a, b; Robinson and Janson, 1987; Rowe, 1996; Kinzey, 1997) suggest that differences in the strength of sexual selection exist between these two species, with *C. apella* being subjected to a stronger degree of sexual selection than *C. albifrons*. These behavioral differences are likely the selective force underlying the observed interspecific differences in ontogenetic patterns of cranial sexual dimorphism.

Because sexual dimorphism exists in several variables related to the masticatory apparatus in both capuchin species, ecological selection may underlie these differences according to Selander's (1972) criteria. However, given the difficulty of determining the presence of ecological selection (Shine, 1989; Janson and Boinski, 1992; Rose, 1994) and the lack of detailed data on sex differences in diet and foraging strategies for these species, future analyses are needed to corroborate the presence of ecological selection. Even then, it may be difficult to partition the roles of sexual and ecological selection. For example, Rose (1994) recently suggested that niche divergence in a congener (*C. capucinus*) is a secondary result of differences in body size due to sexual selection. This is likely to be true in the other capuchin species as well.

Interspecific comparisons

Sexual dimorphism. Hypothesis 3 predicts that *C. apella* possesses a larger degree of cranial dimorphism than *C. albifrons* due to interspecific differences in the strength of sexual selection. Results of several analyses corroborate this hypothesis. An interspecific comparison of sexual dimorphism indices (Table 4) reveals that *C. apella* possesses the larger index in 19 of the 23 cranial variables, even though *C. albifrons* possesses a larger index of body weight dimorphism than *C. apella*, 1.367 and 1.279, respectively (Ford and Davis, 1992). *Cebus apella* possesses moderately larger indices of sexual dimor-

phism in interorbital width, bizygomatic breadth, palate width at canine, palate length, and bimaxillary width. Only in alveolar height does *C. albifrons* possess a moderately larger index.

Greene's (1989) *t*-test indicates (Table 9) that significant interspecific differences in degree of sexual dimorphism are present in seven variables, all favoring *C. apella*. Significant interspecific differences are present in variables of the dental arcade (palate width at canine, palate length, lower facial length) and cranial regions associated with the muscles of mastication (bimaxillary width, bizygomatic breadth, vault height). These findings suggest that adult male tufted capuchins may be able to produce larger forces of mastication compared to male white-fronted capuchins. Only interorbital width cannot be directly associated with the masticatory system. The results of the above analyses, in conjunction with the results of Konigsberg's (1991) multivariate test, corroborate the observation that *C. apella* possesses a more dimorphic cranium than *C. albifrons*.

Not only does *C. apella* appear to be more cranially dimorphic, but significant sexual dimorphism seems to appear earlier in development in *C. apella* compared to *C. albifrons*. A comparison of developmental stages D4, at which both species are approximately 26 months of age (Fleagle and Schaffler, 1982; Galliari, 1985), reveals a large difference in number of significant sexual differences between these two species (Tables 2, 3). Significant sexual differences in *C. albifrons* exist only in palate width (palate width at canine), facial width (bimaxillary width), and facial height (nasion-prosthion). In *C. apella*, a distinct pattern of sexual dimorphism emerges in 1) the dental arcade (palate width at canine, palate width posterior to canine, palate length) and associated masticatory apparatus (bimaxillary width, postorbital constriction, bizygomatic breadth), 2) the lower viscerocranium associated with prognathism (lower facial length, maximum cranial length, basion-prosthion), 3) the neurocranium (anterior basicranial width, bauricular width, bimastoid width, minimum cranial length, basicranial length, neurocranial breadth), and 4) the orbital region (bior-

bital width, interorbital width, orbital width). It is not until the subadult stage (D5), or approximately 42.2 months of age, that a similar pattern is present in *C. albifrons*. This indicates that sexual dimorphism starts developing at an earlier chronological age in *C. apella*.

Cranial form. Hypothesis 4 predicts that the cranium of *C. apella* will be a larger, scaled-up version of *C. albifrons*' cranium. Bivariate growth allometries provide little support for this prediction. Interspecific ontogenetic scaling occurs in only seven of 22 variables (Table 10; Fig. 11); clearly, other processes are acting as well. Significant interspecific position differences are present in eight variables. It appears that *C. apella* is transposed below the *C. albifrons* line in three variables associated with the viscerocranium, whereas *C. apella* is transposed above the *C. albifrons* line in four variables associated with the neurocranium. Departures from ontogenetic scaling occur in the remaining seven variables. An ancestral positive slope gets significantly less positive in palate length (Fig. 13) and interorbital width. From a comparative standpoint, *C. apella* is a neotene in these variables. An ancestral positive slope gets significantly more positive in bimaxillary width, bizygomatic breadth (Fig. 12), and basion-prosthion, whereas an ancestral negative slope gets significantly more negative in biorbital width and orbital width. From a comparative standpoint, *C. apella* is accelerated in these variables.

The prediction of hypothesis 5 that *C. apella* will possess a different pattern of cranial variation in variables associated with mastication does have some analytical support. Many interspecific differences in cranial form seem to be related to differences in diet. For example, several of the departures from interspecific ontogenetic scaling discussed above may be associated with the dental arcade (palate length, basion-prosthion) and development of larger muscles of mastication (bimaxillary width, bizygomatic breadth) in *C. apella*. Results of the DFA (Table 11; Fig. 14) lend further support to this observation. The species are primarily differentiated along function I by variables

relating to the dental arcade and masticatory apparatus (palate width at canine, palate width posterior to canine, bimaxillary width, postorbital constriction). Other interspecific morphological differences are present in the mandible and postcranium that seem to be adaptations that allow the species to live in slightly different ecological niches. In the mandible, interspecific differences in shape exist that may help *C. apella* better process its hard-object diet (Cole, 1992). In the postcranium, Jungers and Fleagle (1980) suggest that differences in body mass distribution are related to differences in locomotor behavior and foraging strategies between the two capuchins. Thus, evidence from the cranium, mandible, and postcranium seems to indicate that some degree of ecological selection has acted to separate these sympatric species. These find-

ings are consistent with the predicted outcome of the competitive exclusion principle (Futuyma, 1986).

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Appendix. Definitions of the 23 cranial measurements

Palate width at canine	Greatest palatal width along the alveolar ridge at the canines
Palate width posterior to canine	Greatest palatal width along the alveolar ridge posterior to the canines
Palate length	Staphylion to infradentale superior
Lower facial length	Midpoint of basioccipital/basisphenoid synchondrosis to infradentale superior
Alveolar height	Nasospinale to infradentale superior
Bimaxillary width	Right zygomaxillare inferior to left zygomaxillare inferior
Biorbital width	Right frontomolare orbitale to left frontomolare orbitale
Interorbital width	Right interorbitale to left interorbitale
Orbital width	Left frontomolare orbitale to left interorbitale
Orbital height	Greatest perpendicular diameter of the left orbital entrance
Postorbital constriction	Narrowest breadth between right and left spheno-parietal sutures behind orbital rim
Bizygomatic breadth	Right zygion to left zygion
Anterior basicranial width	Most inferior point of the curvature of the medial border of the glenoid fossa on the right to the corresponding point on the left
Basioccipital length	Midpoint basioccipital/basisphenoid synchondrosis to basion
Biauricular width	Right auriculare to left auriculare
Bimastoid width	Most lateral point on the mastoid process on the right to the corresponding point on the left
Vault height	Vertex to basion
Maximum cranial length	Opisthocranion to infradentale superior
Minimum cranial length	Opisthocranion to glabella
Basicranial length	Basion to nasion
Basion-prosthion	Basion to infradentale superior
Nasion-prosthion	Nasion to infradentale superior
Neurocranial breadth	Greatest cranial width taken above zygomatic roots on parietal bones

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